LV.—*On the Morphology and Phylogeny of Insects.*

By N. Cholodkowsky *.

"Comparative anatomy will have to confine itself more and more to the raising of problems, while the exact formulation and solution thereof is the province of embryology."—Kleinenberg.

Among the embryological phenomena which are of importance for phylogenetic deductions the segmentation of the germinal streak certainly occupies a prominent position. This will therefore be the appropriate place for the discussion of the question as to the number of the segments of the germinal streak and of their paired appendages. I shall leave out of the question the so-called primary segmentation observed by Ayers, Graber, and Nusbaum—in the first place because it has as yet been but very little investigated, and secondly because I doubt that this primary segmentation was of great phylogenetic importance. For it is quite possible that the early division of the germinal streak into four sections is occasioned by similar causes to those which are responsible for the early appearance of bilateral symmetry in Vertebrates and Arthropods or of the shell in Mollusks, *i. e.* by reaction of the definitive shape of the animal upon the form of the embryo. It may be added that as long ago as 1870 Metschnikow described a similar primary segmentation in *Scorpio*, in which the germinal streak at first divides into three large sections.

The total number of the segments of the germinal streak of Insects is stated by authors to be from sixteen to eighteen, and is said to be at any rate not more than eighteen. The foremost segment, which bears the antennæ, is universally considered to be pre-oral, while the remaining segments are stated to form the primary trunk; the first three of these belong to the head, the fourth to the sixth body-segments to the thorax, and the seventh to the seventeenth to the abdomen. The last (eleventh) abdominal segment is not considered to be entirely homologous with the other metameres, and is termed the "end-segment." The above is the prevalent conception of the Insectan germinal streak at the present time, and in accordance with this are also interpreted the

* Translated from the 'Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg,' vii^{e} série, t. xxxviii. no. 5, pp. 86–101 (St. Petersburg, 1891); being the concluding portion of a memoir by the same author entitled "Die Embryonalentwicklung von *Phyllodromia* (*Blatta*) *germanica*" (*ibid.* pp. 1–120, with six plates).

morphological value of its appendages and their homologies with extremities of other Arthropods. Herein the homology of the anterior end of the embryo in all Arthropods is assumed; the homology of the posterior end is out of the question, for the number of the abdominal segments varies greatly in different Arthropods.

In setting up homologies of the parts of the body and the extremities the question of the value of the foremost cephalic appendages is of special importance, for it is precisely on the basis of the conception of these appendages that attempts have been made to divide the type of the Arthropods into two, three, or four subtypes. In the critical examination of the morphological value of the appendages the innervation of the latter is also taken into account, and justly so. I have no intention of enumerating here the attempts which have been made to homologize the cephalic appendages of Arthropods, since this would lead me too far; it will be sufficient to allude to the fundamental principles of these homologies, which have been accepted by the majority of authors as dogmas. Thus it is considered to be an established fact that (1) the head of Insects consists of four metameres; (2) the antennæ of the Tracheata, partly by reason of their innervation from the supra-œsophageal ganglion, are to be regarded as pre-oral appendages; (3) the cheliceræ of the Arachnida (which were formerly held to be homologues of the Insectan antennæ) are homologous with the mandibles of Insects, since they are originally innervated from a post-oral ganglion, which only subsequently fuses with the supra-œsophageal ganglion; (4) the first (anterior) pair of Crustacean antennæ is homologous with the antennæ of Insects, since to the second pair of antennæ there corresponds a special pair of ganglia which is originally post-oral, though it subsequently fuses with the supra-œsophageal ganglion.

Certain highly important facts have recently become known which, in my opinion, render the justice of the above view of the cephalic appendages of Insects very doubtful. In Chapter IV. of this memoir (p. 43) I have alluded to the fact that the conjecture has already been expressed by Tichomirow * that the Insectan head perhaps consists of six metameres; further, that in the case of *Chalicodoma* even as many as seven embryonic cephalic segments are supposed to exist by Carrière, and that I myself on the basis of my own investigations am inclined to consider that not less than six segments are present in the head of Insect embryos. The

* A. Tichomirow, 'Entwicklungsgesch. des Seidenspinners im Ei' (Moskau, 1882): in Russian.

highly interesting facts communicated by Carrière are unfortunately stated only too briefly; besides this, his figures are somewhat indistinct, and, what is especially to be regretted, his paper contains no transverse sections from the cephalic region such as would make it clear how the seven pairs of ganglia, to which the author alludes, are related to the cephalic extremities. Carrière considers the ganglion frontale to be the nerve-centre of the first (foremost) cephalic segment; as I have already stated, I do not think it possible to homologize the sympathetic ganglia with the centres of the central nervous system. It is further to be remarked that, according to Carrière, the antennary segment is pre-oral, which, however, does not harmonize with his own figures. Carrière states that four pre-oral segments are present, so that only the mandibular and maxillary segments are post-oral. According to my view, however, the homology of the Insectan antennæ with the rest of the ventral extremities is placed beyond all doubt both by their post-oral position, which has been conclusively proved in the case of many Insects, and also by the presence of a mesodermal somite belonging to the antennæ. I am therefore constrained, at least until the appearance of the detailed paper by Carrière, to rely solely upon my own observations upon the development of the cephalic nervous system in *Phyllodromia* and upon Tichomirow's statements as to the embryonic cephalic appendages in *Bombyx mori* (which I find to be confirmed by my own observations upon *Gastropacha pini*). It seems to me that it is sufficiently clear from these observations that, if there is any homology at all between the antennæ of Tracheata and Crustacea, the antennæ of Insects can only correspond to the second pair of antennæ of Crustacea, since the antennary ganglia (the embryonic antennary lobes) of Insects strictly belong to the primary trunk, and, just as in Crustacea, do not become fused with the rudiments of the pre-oral ganglia until later. For the same reason I consider that the cheliceræ of Arachnids are also homologous with the Insectan antennæ. As to further homologies of the mouth-parts and the other extremities of Arthropods, I consider it to be quite impossible to give a comparative table of them at the present time, as has become the usual practice. Such tables are in my opinion premature, since the question of the composition of the Arthropod head proves to be much more complicated than is generally supposed. The very fact, observed by Tichomirow, Bütschli, Carrière, and myself (in *Gastropacha pini*), that small appendages are situated between the antennæ and mandibles, is sufficient to warn us to be cautious and that we

should do better to wait a little before we homologize the mouth-parts of Myriapods, Arachnids, and Insects, not to mention Crustacea. For our knowledge of the development of Myriapods is as yet altogether too scanty, and even the embryology of Insects and Spiders needs completion. Under such conditions it would be far too daring to attempt an homologization of the mouth-parts of Arthropods at present. One thing I believe is certain, namely that the antennæ of Insects, and in all probability of the Tracheata in general, are true homologues of the appendages of the trunk, and therefore do not correspond to the pre-oral antennæ of *Peripatus*. It is also hardly open to doubt that the group Acerata (Pœcilopoda and Arachnida) established by Kingsley does not correspond with its name, for there exists no reason at all for considering the cheliceræ to be not homologous with the Insectan antennæ. There is also no justification for Lang's proposed division of the Tracheata into Antennata (Myriapoda and Hexapoda) and Chelicerata (Arachnida), since the Arachnida, on the basis of the development of the cephalic extremities, are not separable from the Antennata.

Among other appendages of the germinal streak of Insects those belonging to the abdomen are also very interesting, and I will now discuss them somewhat more in detail. As we have seen (Chapter III.) the embryo of *Blatta germanica* possesses eleven pairs of abdominal appendages, which, according to all appearance, are completely homologous with the thoracic legs. It is here my intention to consider those abdominal appendages which persist for a longer time in the post-embryonic development, such as the pro-legs of caterpillars and Tenthredinid larvæ, the abdominal appendages of the Thysanura, &c.

With reference to the abdominal appendages of *Campodea* and *Machilis*, the prevalent view for a long time was that they are homologous with the true legs. Only a few investigators, such as Burmeister *, declared against this theory. Considerable doubt has recently arisen as to the significance of these appendages as rudiments of legs; for certain authors believe that they correspond not to the legs, but to the coxal appendages, which are also present upon the thoracic legs. If this view, which is based exclusively upon anatomical facts, is correct, abdominal legs provided with coxal appendages must nevertheless exist in embryonic life in the case of *Machilis* and *Campodea* also and be able to subsequently disappear, leaving only their coxal appendages behind. Con-

* Burmeister, 'Handbuch der Entomologie,' Bd. 2, 1838, p. 454.

siderable attention has been bestowed upon the abdominal appendages of Insects by Dr. Haase, who recently published a detailed treatise * upon this subject. Unfortunately Dr. Haase's very interesting paper takes zoographical and anatomical facts too exclusively into consideration; it pays but little attention to comparative embryology. In my opinion, however, it is altogether impossible to set up homologies without constant reference to the facts of embryology. For instance, while Haase decides the question as to the abdominal styles of *Machilis* and *Campodea*, which is altogether in dispute, because it has not yet been embryologically investigated, by declaring them to be coxal appendages, he also assigns to the same category the so-called styli of the Orthoptera, whilst partly appealing to my own investigations, which are stated by him to show that the styli "only arise from dermal papillæ considerably later than the rudiments of the legs, and even than those of the cerci." I am bound to declare that neither from my figures † nor from my preparations, which were at his service, was it possible for Dr. Haase to draw such a conclusion. The styli do not arise from "dermal papillæ," but consist, like the rest of the extremities, of ectoderm and mesoderm, and their cavity communicates with that of the somite to which they belong. Moreover, it is indeed true that they arise some time after the thoracic legs, but not later than the cerci. The truth may possibly be that for the earliest rudiments of the cerci Haase mistook the caudal lobes, which subsequently undergo degeneration and are almost entirely absorbed in the formation of the cerci, as has already been described by Tichomirow in the case of *Bombyx mori*. The sole difference between the styli and the cerci on the one hand, and the rest of the abdominal appendages on the other, consists in the fact that the latter soon disappear, while the former persist in post-embryonic development. I have therefore no doubt that the styli in *Phyllodromia* (and, as is highly probable, in all Orthoptera) are genuine rudiments of limbs, and do not correspond to the abdominal styles of *Machilis* and *Campodea*, in the event of Haase's view as to the value of the latter as coxal appendages being correct.

It is true that with regard to the cerci certain doubts

* Haase, "Die Abdominalanhänge der Insekten mit Berücksichtigung der Myriapoden," Morphol. Jahrbücher, Bd. xv., 1889, pp. 331–435, Taf. 14, 15.

† N. Cholodkowsky, "Studien zur Entwicklungsgeschichte der Insekten (n. Nachtrag dazu)," Zeitschr. f. wiss. Zool. Bd. 48, pp. 89–100 and 301–302, Taf. viii.

exist, which, however, are perhaps more apparent than real. Thus the last (tenth) abdominal segment of *Machilis* bears three long-jointed appendages which are similar to one another. If the two lateral appendages correspond to the cerci of the Orthoptera, which is hardly open to doubt, what is the value of the third median appendage? Haase expresses the conjecture that this represents nothing else than a much elongated and secondarily jointed end-segment (anal covering-piece). This explanation is a very plausible one. The best proof of the fact that the segments of the Insect body may exhibit secondary (superficial) segmentation is furnished by certain larvæ, such as, for instance, that of *Chardiophorus*, which exhibits twenty-six apparent segments (behind the head), that of *Thereva*, in which seventeen apparent abdominal rings are visible, and others (according to Perris). But it is self-evident that a definite judgment upon the median terminal filament of *Machilis*, Ephemeridæ, &c. cannot be pronounced until the embryology of these forms has been investigated. Another very interesting example is furnished by the genus *Tridactylus*, Oliv. (*Xya*, Latr.), in which the tenth abdominal segment bears two pairs of cerci (ventral and dorsal). In this case the ventral cerci perhaps correspond to the rudiments (which in other Insects, as also in *Phyllodromia*, undergo degeneration) of the tenth embryonic abdominal segment, which subsequently fuses with the eleventh. This question has likewise to be decided by embryological investigation.

Thus we see that the difficulties as to the interpretation of cerci, to which reference has been made, are at any rate capable of more or less plausible explanations; on the other hand, the development of the cerci in *Phyllodromia* shows so clearly that they are equivalent to the antennæ and the rest of the ventral extremities that I can discover no reason whatever for not regarding them as homologous with the thoracic limbs. In any case such an interpretation of the cerci appears to me to have a much better foundation and to be less arbitrary than, for instance, the comparison with the furcal appendages of *Apus* or the anal feelers of Polychætes (Haase).

Of the highest interest are the ventral appendages of Poduridæ, that is to say the springing-fork and the so-called ventral tube. Haase considers the fork to be equivalent to the abdominal styles of *Machilis*, and therefore not homologous with the limbs. But it has already been shown by Uljanin* that the springing-fork of the Poduridæ arises from

* B. Uljanin, "Beobachtungen über die Entwicklung der Poduren,"

two abdominal appendages, which are in every respect similar to legs, so that their homology with the thoracic limbs is hardly open to doubt. With regard to the ventral tube it is supposed by Haase that this corresponds to the "ventral sacs" of *Machilis*, *Scolopendrella*, *Campodea*, &c., wherein he again disregards embryological facts; for it was proved by Uljanin that the ventral tube develops from two anterior abdominal appendages, which are quite similar to, and almost certainly homologous with, the thoracic legs, while the ventral saccules, *e. g.* in *Scolopendrella*, occur on the same segments as those on which limbs are also present, and therefore cannot be homologous with the legs. With regard to the pyriform appendages of the first abdominal segment of certain Insect embryos Haase expresses himself very vaguely; for while he considers their homology with the ventral saccules to be also somewhat doubtful, he nevertheless believes that they possess a similar (respiratory) function, and that "it is probably a latent ancestral character that allows these structures, which are so entirely analogous to one another, to arise once more at the same places." Embryology, however, shows most distinctly that the pyriform appendages develop from typical leg-like structures, indisputably homologous with the thoracic limbs, and that therefore there can be no question of homology with the ventral saccules of Myriapods and Thysanura. As to the function of the pyriform appendages, this is in all probability the same as that of the ventral tube of the Poduridæ, which, according to Haase, climb up glass by the help of this organ (though they are also capable of doing so without its assistance). That the pyriform organs are adhesive was the conclusion previously arrived at by Rathke *, according to whom in extracting embryos of *Gryllotalpa* from the embryonic envelopes the "mushroom-shaped bodies" are easily detached and remain sticking to the envelopes †. The latest statements of Wheeler ‡, Graber §, and Nusbaum ‖

Nachrichten d. Moskauer Gesellsch. d. Liebhaber von Naturwissensch. &c., 1875, Bd. 16, Lief. 3, pp. 1–10, Taf. iii.–v. (in Russian).

* Rathke, "Zur Entwicklungsgeschichte der Maulwurfsgrille," Arch. f. Anat. u. Physiol. 1844, pp. 27–38, Taf. ii. figs. 1–5.

† Rathke was also the first to observe the facetted surface of these appendages.

‡ W. M. Wheeler, "The Embryology of *Blatta germanica* and *Doryphora decemlineata*," Journal of Morphology, vol. iii. 1889, pp. 293–374, pls. xv.–xx.

§ Graber, "Ueber den Bau und die phylogenetische Bedeutung der embryonalen Bauchanhänge der Insecten," Biol. Centralbl., Bd. ix. 1889–1890, pp. 355–363.

‖ J. Nusbaum, "Die Entwicklung der Keimblätter bei *Meloë proscarabæus*," Biol. Centralbl., viii., 1888, p. 449.

also agree with this. But if these organs exhibit a glandular character it does not yet follow that they have a respiratory function. New experiments conducted by Haase upon the ventral saccules and the ventral tube prove that these organs in the expanded and extended condition become filled with blood; this takes place especially in a damp and warm atmosphere. Haase concludes from this that they represent gills. It is not impossible that in certain cases the pyriform abdominal appendages of Insect embryos may also subserve the respiratory function; such is certainly not the case in *Blatta germanica*, however, for here the appendages in question contain no cavity whatever. However this may be, embryology shows us quite unmistakably that the original shape of these appendages is leg-like, and that therefore their primitive function was an ambulatory one; it is not until later that they change their form and become, owing to enormous development of the ectoderm cells, glandular adhesive organs; if at the same time a cavity is preserved in them, they may perhaps to a certain extent also assume the function of respiration. It is very interesting to compare these glandular appendages with the abdominal appendages of the Spiders, which become spinnerets. In the Spiders, according to the beautiful observations of Morin *, at the tip of the appendage a glandular depression (the future spinneret) is formed, which is altogether similar to the depressions described by Nusbaum † in the abdominal appendages of *Meloë* ‡.

I now proceed to the consideration of the other abdominal appendages which persist in post-embryonic life. To this category belong both the so-called pro-legs of Lepidopterous and Tenthredinid larvæ, and also the abdominal appendages of other Insect larvæ. In the paper which has been cited above Herr Haase has collected a large number of facts bearing on this point, so that I can dispense with their enumeration. I therefore address myself at once to the abdominal legs of caterpillars.

As is well known, as long ago as 1869 the view was expressed by Brauer § that multiped insect larvæ are to be

* Morin, "Zur Entwicklungsgeschichte der Spinnen," Biol. Centralbl., vi. Bd., 1887, pp. 658–663. (Also in Russian, with plates: Odessa, 1887.)

† *Loc. cit.*

‡ Whether the eversible caruncles described by Gerstaecker ("Ueber das Vorkommen von ausstülpbaren Anhängen am Hinterleibe von Schaben," Archiv für Naturgeschichte, 27 Jahrg., i. Bd., 1861, pp. 107–115) in *Corydia* also belong here is very doubtful.

§ Brauer, "Betrachtungen über die Verwandlung der Insekten im Sinne der Descendenz-Theorie" (with one plate), Verh. zool.-bot. Ges. Wien, Bd. 19, 1869, pp. 299–318.

regarded as secondary forms which are derivable from the primary *Campodea*-like larva and have arisen by the process of adaptation. The theory started by Brauer was supported by Packard * and Lubbock †, and has been the generally accepted one hitherto. At the time when Brauer published his little paper, which has met with so much success, our knowledge of the embryonic development of insects was still very scanty, since Kowalevsky's ‡ memoir, by which new paths were opened out, and Bütschli's § paper, in which the presence in an insect embryo of numerous abdominal appendages was asserted for the first time, were not published until 1871 and 1870 respectively. This, as it seems to me, explains the favourable reception of Brauer's hypothesis, with which, as I shall show, the embryological facts are decidedly at variance. That this hypothesis has hitherto maintained its importance for the majority of zoologists and is constantly repeated in text-books is in my opinion accounted for by the insufficiency of the embryological statements on the question, as also by the fact that certain valuable papers are incompletely known; thus, for instance, Tichomirow's memoir upon *Bombyx mori*, because it is written in Russian, has only become more fully known to foreign students within the last few years. But although I will not deny that the embryology of Insects, and of Lepidoptera in particular, still requires completion, nevertheless I venture to assert that precisely on the subject of the abdominal appendages our knowledge is already satisfactory. The facts bearing upon this were communicated by Kowalevsky, Tichomirow, and Graber. Kowalevsky, who, *inter alia*, investigated the embryology of *Smerinthus populi*, figures ten pairs of perfectly distinct abdominal appendages upon the germinal streak of this moth. Tichomirow describes and figures in *Bombyx mori* small but "distinct" appendages on all the abdominal segments with the exception of the first; in subsequent stages (when the cephalic segments become fused together) only the appendages of the third to the sixth segments and of the eleventh segment (which afterwards fuses with the tenth and ninth) are preserved and undergo further development, while the

* Packard, 'The Ancestry of Insects' (Salem, 1873).

† Lubbock, 'Ursprung u. Metamorphosen der Insekten' (Jena, 1876). ['On the Origin and Metamorphoses of Insects' (London, Macmillan and Co., 1883).]

‡ A. Kowalevsky, "Embryologische Studien an Würmern und Arthropoden," Mém. Ac. Sc. Pétersb. 7, xvi. no. 2, 1871, 70 pp., 12 plates.

§ Bütschli, "Zur Entwicklungsgeschichte der Biene," Zeitschr. f. wiss. Zool. Bd. 20, 1870, pp. 519–564, 4 plates.

rest atrophy and finally disappear without leaving a trace behind. Graber studied *Gastropacha quercifolia*, in which moth we are told that the abdominal appendages do not appear until a relatively very late period (when the four cephalic segments have become fused together), and then only on those segments on which they are also present in the caterpillar; so that the series of embryonic abdominal appendages is not a continuous one. From this Graber concludes, erroneously referring to Tichomirow (the Russian text of Tichomirow's paper was clearly unintelligible to him), that the pro-legs of caterpillars are not homologous with the thoracic legs, and represent secondary formations. At the same time he is nevertheless prepared to allow that if a continuous series of abdominal appendages is actually present in the embryo they are homologous with the thoracic legs. In my opinion there is no question that the latter is actually the case; for, in the first place, the accuracy of Kowalevsky's assertion is hardly open to doubt, since it is highly improbable that so cautious and delicate an investigator as Kowalevsky, whose observations have almost without exception been confirmed by all students, could go wrong in so simple a question; and, secondly, Tichomirow's statements also are very ample and definite. It is true that Graber says that his drawings are "indistinct;" but only the appendages of the eleventh abdominal segment are indistinct, or, strictly speaking, not shown at all, in Tichomirow's fig. 26, while the rest of the abdominal appendages are indeed faintly outlined but perfectly distinct. Particularly full and exact, however, is the description of the abdominal appendages given in the text (pp. 41–42). To this I can further add that, on the basis of my own investigations upon the germinal streak of *Gastropacha pini*, I can entirely confirm Tichomirow's account, since in this moth also at a very early stage in its development a continuous series of very small but yet distinct abdominal appendages is observable, and the figure given by Tichomirow for *Bombyx mori* (fig. 26) also applies in every detail to *Gastropacha pini*.

But if, with reference to the external development of the Lepidopterous embryo, we were absolutely unacquainted with anything but the published observations of Graber upon *Gastropacha quercifolia*, it would, I believe, nevertheless not follow therefrom that the pro-legs of caterpillars are "secondary" structures; for whereon should such a conclusion be founded—upon the late appearance of the abdominal appendages or upon the fact that the series thereof is not an unbroken one? But late appearance in itself cannot be

accepted as a proof of the secondary nature of an organ, since in the appearance of the organs in the embryonic development of closely allied animals no definite sequence whatever is observable; it is possible for one and the same organ or system of organs to appear in one animal very early but in another very late. Thus, for instance, in *Apis* the pores for the stigmata are almost the very earliest differentiations of the segmented germinal streak, while in *Blatta germanica* they are not observable until after the segmentation of the extremities has begun. But does it follow from this that the stigmata are primary in Hymenoptera but secondary in Orthoptera? With regard, however, to the discontinuity in the series of abdominal appendages and their appearance only on those segments on which pro-legs are present in the caterpillar, this fact, which has hitherto only been observed in the embryo of one moth, does not yet prove in itself that the pro-legs are secondary structures. Instead of setting up the hypothesis that the caterpillars had acquired their abdominal appendages in post-embryonic development, and that subsequently the first appearance of these organs was transferred to early (embryonic) stages, we are just as much justified in assuming that in the embryo, which originally possessed a continuous series of abdominal appendages, later on rudiments of only those appendages began to appear which also persisted in post-embryonic development; further, that the suppression of the rest of the abdominal extremities resulted from the same cause as that which in the embryo of other Insects is responsible for the non-appearance of the whole of the abdominal feet, *i. e.* in consequence of disuse. The second hypothesis is even *à priori* not less probable than the first; but, by the fact that in certain lepidopterous embryos a continuous series of abdominal legs is actually present, it is completely confirmed and is certainly the only correct one. When discussing my paper upon the external development of *Blatta germanica*, Prof. Emery, *inter alia*, writes as follows*:—"The abdominal legs of lepidopterous caterpillars may quite well have developed afresh through reversion in phylogeny from the embryonic rudiments which quickly disappear in the case of other insects, and those caterpillars may with much probability be derived from primitive *Campodea*-like forms. It is probable that cases of atavism of this kind play a much more important part in phylogeny than is generally supposed. Primitive structures are developed

* Emery, "Neuere Arbeiten über die Phylogenie der Insekten," Biol. Centralbl., Bd. ix., 1889–90, pp. 396–405.

afresh through new adaptation from a rudimentary or even latent condition, and thus new conditions of organization arise which, with equal justice, may be regarded as either primitive or secondary." I give this quotation here in order to point out that some years ago I already drew attention to the possible (and probable) great importance of atavism in ontogeny and phylogeny * by designating the cases of this class as "normal periodic atavism." While I thus agree with Herr Emery in considering it, as a matter of principle, a very probable possibility that organs which are secondary in ontogeny may be homologous with those which are primary in phylogeny, I nevertheless regard it as superfluous, and even impossible, to apply this view to caterpillars. That the polypod caterpillars cannot be derived from hexapod (*Campodea*-like) larvæ is proved at once by the fact that the latter may themselves be polypod in their embryonic development (e. g. *Hydrophilus*). The entire difference between hexapod and polypod Insect larvæ thus depends upon the circumstance that in the former the abdominal legs atrophy before the animal is hatched, while in the latter they persist in post-embryonic development. It is clear from the embryology of Insects that the polypod larvæ cannot be derived from the hexapod; on the other hand, however, palæontology teaches us that the oldest Insects possessed an incomplete metamorphosis, and therefore were hexapod after leaving the egg, and that consequently also the hexapod larvæ are not to be derived from polypod forms. Thus the only alternative is to suppose, what is also most natural, that **the hexapod as well as the polypod larvæ in different orders of Insects have arisen independently of one another.**

Having discussed the question of the abdominal extremities of caterpillars, I must also briefly allude to the abdominal appendages of the other Insect larvæ. As I have stated above, Dr. Haase has gathered together in his new paper† almost all the instances which belong to this category. Unfortunately he at the same time utilizes for his deductions almost exclusively zoographical and anatomical facts, while on the other hand he appears to regard the results of comparative embryology as superfluous. Thus, for instance, it is enough for him to establish the fact that the abdominal appendages do not lie directly in prolongation of the line of

* Cholodkowsky, "Sur la morphologie de l'appareil urinaire des Lépidoptères," Archives de Biologie, t. vi., 1885, pp. 497–514, pl. xvii.; "Sur les vaisseaux malpighiens des Lépidoptères," Comptes Rendus Acad. Paris, t. xcviii. pp. 631–633, t. xcix. pp. 816–819 (1884).

† *Op. cit.*

the thoracic legs, but somewhat to the side of or inwards from it, in order to reject the homology between these appendages and the thoracic legs. It appears to me, however, that the acceptance or rejection of homologies is, in the great majority of cases, absolutely impossible without reference to embryology, which alone can show us whether the appendages in question proceed or not from abdominal legs, of which rudiments are formed in the embryo. If it is precisely the embryological facts that are wanting the question must remain undecided, and all conclusions are premature. Thus, for example, many Tenthredinid larvæ possess numerous abdominal appendages which appear in the highest degree similar to those of lepidopterous caterpillars. But since the embryology of the saw-flies, apart from a few extremely incomplete statements by Packard *, is as yet unknown, the nature of the appendages in question, notwithstanding their great similarity to those of caterpillars, cannot be precisely determined.

Of great interest is the question as to the morphological value of the so-called **gonapophyses**, *i. e.* the male copulatory organs, ovipositors, the sting of the Hymenoptera, &c. Under the head of gonapophyses I also include, *inter alia*, the male *appendices copulatarii* of the Lepidoptera. Some authors, such as Huxley and Dewitz, consider the gonapophyses to be the homologues of legs; others, such as Claus, do not venture to express themselves positively upon this question, and merely remark that the homology of the gonapophyses with the legs is not proved; finally, certain authors decisively reject this homology. Against the homologization of the gonapophyses with legs various evidence can be adduced. Thus, for instance, in *Machilis* ventral styles are also found upon the abdominal segments which bear the gonapophyses, so that these segments are each provided with two pairs of appendages. We have already seen that the question of the value of the ventral styles of the Thysanura cannot be decided, on account of our ignorance of their embryological development. But apart from this, the fact of the presence of two pairs of appendages upon one segment is not in itself an argument against the homologization of these appendages with the legs. In the first place it has been shown by the beautiful investigations of Uljanin upon the post-embryonic development of the bee † that it is possible for appendages

* Packard, "Embryological Studies on Hexapodous Insects," Memoirs of the Peabody Academy of Science, v. 1, no. 3, 1872, 17 pp., 3 plates.

† B. Uljanin, "Zur postembryonalen Entwicklung der Biene," Protokolle der Sitzungen der Moskauer Gesellschaft der Liebhaber von Naturwissenschaft, Anthropologie und Ethnographie, Jahrg. ix., 1872, Moskau, pp. 17–32, Taf. ii. v. (in Russian).

which are originally simple to subsequently split longitudinally, whereby two pairs of appendages are produced, which all taken together may be homologous with one pair of legs. In the second place, if the hypothesis that the ventral styles correspond to the coxal appendages is correct, the ventral styles of the eighth and ninth segments in *Machilis* may represent the coxal appendages detached from the trunk of the extremities. Other objections against the homologization of the gonapophyses with the legs are based upon the late appearance of the former, which are therefore supposed to be "secondary" structures. I have already had occasion to point out that more or less late appearance of the organs in development is of little importance for the setting up of homologies; I am convinced that even organs which first appear in post-embryonic life may be equivalent to those which are developed at a very early stage, since there really exists no radical difference between embryonic and post-embryonic development. If certain organs may be referred to purely post-embryonic adaptation, we are nevertheless not bound to consider as phylogenetically secondary all structures which are post-embryonic in appearance. In the particular case of those Insects in which the development of the gonapophyses has been sufficiently investigated (*e. g.* the bee) the homology of the latter with the legs appears to be precisely very probable. According to Uljanin*, in the bee the sting develops from two pairs of appendages at the posterior end of the abdomen, and the hindermost appendages very quickly split longitudinally. It is stated by Bütschli † that in the embryo of the bee the two posterior pairs of abdominal appendages are especially developed. Grassi ‡, too, alludes to these appendages, although (contrary to Bütschli) he denies the presence of the rest of the abdominal extremities. It appears that these hindermost abdominal appendages subsequently greatly diminish in size, so that immediately before hatching takes place they are represented by flat ectodermal disks (Kowalevsky §). It is only after the second ecdysis of the larva (according to Uljanin) that they commence to grow bigger, and, what is especially interesting, they even exhibit an indistinct segmentation. The development of these abdominal appendages therefore retrogrades somewhat towards the end of embryonic life, and it is only in post-

* *Op. cit.* † *Op. cit.*

‡ B. Grassi, "Intorno allo sviluppo delle Api nell' uovo," Atti dell' Acad. Gioenia di Scienze Natural. in Catania, S. 3°, vol. xviii., 1884, 78 pp., 10 plates.

§ *Op. cit.*

embryonic development that further progress takes place. According to Haase these appendages cannot be homologous with the legs, because their earliest rudiments are purely ectodermal. "This view," he writes, "which appears to be supported by Grassi also, was expressed for the first time in 1872 by Uljanin, who demonstrated the development of the gonapophyses from subcutaneous imaginal disks." This reference to Uljanin, which, as I shall immediately show, is quite unjustifiable, is doubtless due to Dr. Haase's ignorance of the Russian tongue; for, contrary to what is stated by Dr. Haase, Uljanin expresses his deep conviction that the parts of the sting are homologous with the legs and that the lancets correspond to one, and the quadrate plates together with the sheath to another pair of legs. It is also proved by Uljanin that the thoracic legs likewise develop from subcutaneous imaginal disks, so that no difference really exists between the mode of development of the thoracic legs and that of the abdominal appendages. There is consequently no reason for not regarding the bee's sting as homologous with the thoracic legs.

The embryology of the bee also furnishes excellent evidence of the justice of the view which, as I have stated above, I expressed years ago *, that organs also which are really secondary in ontogeny may have just the same morphological and phylogenetic value as undoubtedly primary structures. The thoracic legs of the embryo of the bee are so strongly developed that they have been observed by every one of the embryologists who have investigated the development of the animal in question. These legs diminish in size as the development of the embryo proceeds, and become transformed into flat ectodermal disks (Kowalevsky). It is only in the course of larval and pupal life that they undergo further development and become definite legs. The thoracic legs of the bee are therefore secondary according to their mode of development; yet it will scarcely occur to any one to doubt their homology with the thoracic legs of other Insects. Just as "secondary" are also the thoracic legs of the bark-beetles (according to the investigations of Packard †, which I can confirm from my own studies), of the flea (according to Bal-

* Cholodkowsky, "Sur la morphologie de l'appareil urinaire des Lépidoptères," Archives de Biologie, t. vi., 1885, pp. 497–514, pl. xvii.; "Sur les vaisseaux malpighiens des Lépidoptères," Comptes Rendus Acad. Paris, t. xcviii. pp. 631–633, t. xcix. pp. 816–819 (1884).

† Packard, "The Development of the Bark-Beetles (*Xyleborus* and *Hylurgops*)," U. S. Department of Agriculture, 3rd Report of the Entomological Commission (Washington, 1883), pp. 280–282, pl. xxii.

biani *), and probably of a large number of Insects whose larvæ are apodous. The cephalic appendages (antennæ and maxillæ) of the Muscidæ are likewise subject to degeneration in the larval stage, and subsequently develop a second time. Among the internal organs all parts which in the pupal stage are destroyed by histolysis are also "secondary" in the adult. Similar processes may also be observed among the Crustacea. Thus in the Stomatopoda (in *Ericthus* according to Claus) three posterior pairs of thoracic legs do not appear until the end of the larval stage, while the third to the fifth pairs are developed very early, to subsequently atrophy and then reappear. With reference to this remarkable phenomenon Lang † writes as follows:—"The first start towards the formation of the whole or of the majority of the typical appendages of the Malacostraca, which we here describe and which is subsequently annulled, is without doubt to be ascribed to the power of heredity. The temporary disappearance of a portion of the extremities is most probably a case of adaptation to the special conditions of larval existence, which are so different from those of the adult animal. If, however, in the course of time the first fruitless and useless start became gradually weaker, and were finally entirely omitted, we should in the case of Loricata and Stomatopoda meet with phenomena entirely similar to those in the development of the Brachyura, where the formation of the last five thoracic segments and their appendages takes place so extraordinarily late." I would willingly subscribe to these words, and I consider that Lang's conclusions are also to be extended to other animals, such as, for example, the Insects. It is evident that that which is secondary in ontogeny is by no means always also phylogenetically secondary. Altogether it appears to me that the conception of what is secondary is only too often misused: should any phenomenon be inconvenient to an author for the working-out of his theories, he simply declares it to be "secondary," and thinks that in so doing he has disposed of the whole question.

The development of the male gonapophyses has unfortunately received much less investigation than that of the oviduct and of the sting. The very interesting "*forcipes*" of the humble-bees represent very well developed and even segmented appendages ‡, which quite convey the impression

* Balbiani, "Sur l'embryogénie de la puce," Comptes Rendus Acad. Paris, t. lxxxi., 1875, pp. 901–904.

† Lang, 'Lehrbuch der vergleichenden Anatomie,' Abth. 2 (Jena, 1889).

‡ Schmiedeknecht, "Monographie der in Thüringen vorkommenden

of somewhat modified legs. Packard's investigations*, however, appear not to confirm the homology of these appendages with the legs, since they are said to develop from three pairs of tubercles which all belong to the ninth segment. Kraepelin likewise rejects the homology of the copulatory organs of the drone (*Apis mellifica*) with the parts of the sting of the female. This question needs further investigation. Matters are somewhat better with regard to the male forcipes of the Lepidoptera. As is well known† these forcipes develop from the hindmost pair of pro-legs of the caterpillar (the so-called claspers); but according to Tichomirow the latter arise from the hindermost pair of the embryonic abdominal appendages, *i. e.* from the appendages of the eleventh segment, and therefore correspond to the cerci of other Insects. For Tichomirow states that the caudal lobes diminish more and more in the course of the development, and finally are almost entirely absorbed in the formation of the hindermost pair of the abdominal legs of the larva, whose ninth abdominal segment arises through the fusion of the sixteenth to the eighteenth embryonic segments. I have shown above that in all probability the cerci are homologous with the true legs; the forcipes of the male Lepidoptera are consequently likewise to be regarded as homologues of the legs. In the adult state they are attached to the ventral half of the ninth abdominal ring, which in many species is greatly modified, but in some preserves its typical annular shape.

The gonapophyses are thus, in certain cases at least, to be considered as homologues of the legs.

In considering the morphology of the germinal streak of Insects I cannot refrain from touching upon the question of the relation of the germinal streak and the embryonic envelopes to the Trochosphere-theory. We know that in 1878 B. Hatschek produced a scheme of the formation of the Annelidan body, according to which the foremost or cephalic segment is contrasted with the whole of the remaining body-segments, as forming the trunk. This scheme has recently also been applied to the germinal streak of Insects, which, according to Haase, is composed, (1) of the antennæ-bearing

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Arten der Gattung *Bombus*," Jenaische Zeitschrift, 12 Bd., 1878, pp. 303–430, with two plates.

* Packard, "Observations on the Development and Position of the Hymenoptera," Ann. & Mag. Nat. Hist. xviii., 1866, pp. 82–99.

† Barthelemy, 'Recherches d'anatomie et physiologie générales sur la classe des Lépidoptères' (Toulouse, 1864), 11 planches; Künckel, "Signification morphologique des appendices servant à la suspension des chrysalides," Comptes Rendus Acad. Paris, t. xci., 1880, pp. 395–397.

"frontal piece" (the "cephalic segment" of Hatschek); (2) of a series of limb-bearing metameres, which are homologous with one another; and (3) of a cerci-bearing end-segment. I have already adduced evidence against the view that the antennæ and cerci are not homologous with the legs, and I consider it superfluous that I should here revert to the question. I will merely point out that although the antennæ are not pre-oral and belong to the primary trunk, nevertheless the pre-oral segment is actually present and is separated from the rest of the body by the antennary groove. Whether this pre-oral segment is comparable to the body of the Trochosphere or not is very questionable. On the one hand, this comparison is not to be rejected because the pre-oral segment contains no cœlomic cavities, while on the other the Insects have certainly receded so far from their ancestors the Annelids that a repetition of the Trochosphere stage in their development may also be entirely omitted. The fact that the pre-oral ganglia develop from rudiments which are separated from the ventral chain is scarcely to be considered of such high importance as has been ascribed to it by certain investigators *, since, as we have already seen, each ganglion of the ventral chain may also arise from a separate rudiment. That the pre-oral segment contains no cœlomic cavities is perhaps explained by the rudimentary character of its appendages (labrum), and it is at the same time also advisable to wait for detailed investigations upon the development of this segment, in which perhaps, as in the "end-segment" of *Blatta germanica*, rudimentary cœlomic cavities will be discovered.

As regards the embryonic envelopes, the question as to their morphological value is answered in very different ways. P. Mayer † regards the formation of the embryonic envelopes as a summary ecdysis on the part of the embryo, a view which is also adopted by Balfour. Tichomirow ‡ and Emery § consider it possible to compare the embryonic envelopes of Insects with the carapace of Crustacea. Kennel ||

* Schimkewitsch, "Étude sur le développement des Araignées," Arch. de Biologie, t. vi., 1885, pp. 515–584, pls. xviii.–xxiii. The same in Russian, St. Petersburg, 1886.

† P. Mayer, "Ueber Ontogenie und Phylogenie der Insekten," Jenaische Zeitschr. x., 1876.

‡ A. Tichomirow, 'Entwicklungsgeschichte des Seidenspinners im Ei' (Moskau, 1882: in Russian).

§ Emery, "Referat über die Arbeiten von Korotnew und Grassi," Biol. Centralbl., Bd. v., 1887, pp. 656–657.

|| Kennel, "Entwicklungsgeschichte von *Peripatus*," Arbeiten a. d. zool.-zoot. Inst. in Würzburg, Bd. 7, 1885, pp. 95–200, Taf. v.–xi., Bd. 8, 1888, pp. 1–93, Taf. i.–vi.

considers the same structures to be rudiments of the Trochosphere. Will * suggests a new hypothesis, which at first sight appears very simple and plausible; for, while comparing the internal germinal streak of Insects with the germinal streak of Myriapods (which, as is well known, increases very greatly in length, and finally bends together in the middle and becomes invaginated into the nutritive yolk), he considers the amnion of Insects to be homologous with the posterior half of the Myriapod germinal streak. The Insects with an internal germinal streak would consequently be phylogenetically older than those with an external one (contrary to the opinion of P. Mayer, according to whom the reverse is the case, and the Insects with an external germinal streak are the older). Of all these hypotheses that which is proposed by Tichomirow and Emery appears to me to be least happy. The entire results of embryology and comparative anatomy compel us to suppose that the Crustacea must have had an origin separate from that of the rest of the Arthropoda; so that a repetition of the Crustacean carapace in the development of Insects appears to be simply impossible. Will's hypothesis is hardly applicable to those Insects in which the cephalic fold (which, according to Will, is a secondary formation) of the amnion constitutes almost by itself the entire amnion (*Apis*), while the caudal fold is very little developed; it is also very improbable that the cephalic and caudal folds of the amnion, which are so similar in their formation, were of quite different origin. Until the appearance of Graber's paper † P. Mayer's hypothesis seemed to me to be the most probable; according to Graber, however, the amnion in *Melolontha* consists not merely of ectoderm but also of mesoderm, which is surely irreconcilable with the interpretation of the amnion as a cast-off skin. Kennel's view, on the contrary, appears to find confirmation in this remarkable fact. Altogether the above-mentioned hypothesis of Kennel seems to me to be the only one against which no evidence of importance can be adduced. I therefore gladly allow with Kennel that the embryonic envelopes are no new formation,

* L. Will, "Entwicklungsgeschichte der viviparen Aphiden," Zool. Jahrb., Abth. f. Morphol. Bd. iii., 1888, pp. 201–286, Taf. vi.–x. (Also Arb. zool.-zoot. Inst. Würzb., Bd. 6, 1883, "Ueber die Embryonalentwicklung d. viv. Aphiden," Sitz.-Ber. naturf. f. Ges. Rostock, 24 mai, 1887; Arch. Ver. Freund. Naturg. Mecklenb., 1887, 41 Jahrg. 1888; "Zur Entwicklungsgesch. d. vivip. Aphiden," Biol. Centralbl., viii., 1888, no. 5.)

† Graber, "Vergl. Studien über die Keimhüllen und die Rückenbildung der Insekten," 54 pp., 8 plates, 32 woodcuts, Denkschriften d. math.-naturw. Classe Kais. Akad. Wiss. Wien, 1888.

but, on the contrary, represent what is oldest in the Insect embryo. This view is also in accordance with the fact that it is precisely in those Insects (Diptera) which have undoubtedly departed furthest from the primitive forms that the embryonic envelopes are most feebly developed and are almost entirely wanting.

To sum up the whole of what has been stated above, I advance the following main theses :—

1. The head of Insects contains more than four protozonites, probably six, of which one is pre-oral, but the rest are post-oral.

2. The antennæ of Insects belong to the first post-oral segment and are entirely homologous with the remaining ventral extremities. They do not correspond to the antennæ of *Peripatus*, but probably to the cheliceræ of Spiders, and perhaps to the second pair of antennæ of Crustacea.

3. Since the possibility that a number of segments in the germinal streak of different Arthropods have disappeared is not excluded, a homology of the mouth-parts of the different classes of Arthropoda cannot at present be set up.

4. The abdominal appendages of the Insectan germinal streak (including the cerci) are homologous with the thoracic legs. Herein it makes no difference whether these appendages are attached to the middle, at the side, at the front, or hind margin (are meso-, pleuro-, pro-, or opisthostatic, in the terminology of Graber), provided only that their cavity is immediately continuous with that of the somite to which they belong. The fact that the abdominal appendages usually remain unsegmented in nowise tends to show that they are not of the nature of limbs, since, for instance, the mandibles also are always unsegmented *.

5. Many of the abdominal appendages of larvæ and perfect Insects are homologous with the thoracic legs, even when they are secondary in ontogeny.

6. The primitive function of the first pair of the abdominal appendages was ambulatory, as also that of the remaining appendages. The ancestors of the Insects were therefore undoubtedly homopod, not heteropod.

7. The many-legged Insect larvæ are to be derived from the six-legged just as little as are, conversely, the hexapod larvæ from the polypod; both forms developed independently of one another.

* Whether the segmented branchial filaments of *Sisyra* and *Sialis* belong to this category is doubtful, but can only be decided by embryological investigations.

8. The embryonic envelopes of the Insects probably correspond to the remains of a Trochosphere.

The above theses convey the leading features of my view as to the phylogenetic relations of Insects. Widely different decisions as to the origin of Insects have been pronounced by authors. The hypotheses dealing with the question are enumerated and criticized at some length in Graber's work 'Die Insekten' * (pp. 66–71) and in Sograf's memoir on the development of *Geophilus* †, so that I can dispense with a comparison of them. I will merely remark that I entirely agree with Graber's opinion upon the *Zoœa*-hypothesis—"a more unsuitable claimant to be regarded as the ancestor of terrestrial Insects ('einen unpassenderen Landkerfcandidaten') could never have been found,"—as well as with Sograf's argument against the Myriapod hypothesis of Haeckel ‡. Quite recently the relationship between Insects and Myriapods has been placed more and more beyond doubt, thanks to the work of Moseley §, Balfour ‖, Kennel ¶, Sedgwick **, and Gaffron †† upon the anatomy and embryology of *Peripatus*, as also to the investigations of Ryder ‡‡,

* München, 1877.

† Sograf, "Zur Kenntniss der Embronalentwicklung von *Geophilus*," Nachr. der Moskauer Gesellschaft der Freunde der Naturwissenschaft &c., Bd. 43, Lief 1, 1883 (in Russian).

‡ Sograf writes:—"The pulli of the Chilognatha correspond to the germinal streak of Insects, provided with six (anterior) pairs of extremities. . . . . Consequently in order that it should be possible to compare the Chilognatha with Insects or Arachnids, it would have to be proved that the hexapodous Chilognathan embryo formerly possessed a far greater number of extremities, all of which atrophied except the three anterior pairs. That such a metamorphosis formerly belonged to the Chilognatha, but was afterwards lost, is very improbable." As we see, the question here also depends upon whether the embryo acquires or loses its legs before or after leaving the egg.

§ Moseley, "On the Structure and Development of *Peripatus capensis*," Phil. Trans. Roy. Soc. London, vol. clxiv. 1874, pp. 757–782, 4 plates.

‖ Balfour, "The Anatomy and Development of *Peripatus capensis*," Quart. Journ. Micr. Sci. vol. xxiii., 1883, 8 plates.

¶ Kennel, "Entwicklungsgeschichte von *Peripatus*," Arbeiten aus dem zool.-zoot. Inst. in Würzburg, Bd. 7, 1885, pp. 95–200, Taf. v.–xi., Bd. 8, 1888, pp. 1–93, Taf. i.–vi.

** Sedgwick, "The Development of *Peripatus capensis*," Quart. Journ. Micr. Sci. vol. xxv. 1885, pp. 449–468, 2 plates, vol. xxvi. pp. 175–211, 3 plates, vol. xxvii. pp. 467–550, 4 plates; "On the Fertilized Ovum of and the Formation of the Layers in *Peripatus*," Proc. Roy. Soc. Lond., vol. xxxix., 1885, pp. 239–244.

†† Gaffron, "Beiträge zur Anatomie und Histologie von *Peripatus*," Zool. Beitr. Schneid. 1 Bd., 1883–1885, pp. 33–60 and 145–165, 9 plates.

‡‡ Ryder, "The Structure, Affinities, and Species of *Scolopendrella*," Proc. Ac. Nat. Sci. Philadelphia, 1881, pp. 79–86.

Haase, Nassonow *, Grassi †, Oudemans ‡, and others upon the morphology of the lower Insects and Myriapods. The fact, which was brought forward by myself for *Blatta germanica* and confirmed by Graber, of the remarkable division of the cavity of each somite into three sections, one of which is, in my opinion, homologous with the segmental funnel of *Peripatus*, seems to decide the question still more definitely in favour of the derivation of the Insects from homo- and polypod and, probably, *Scolopendrella*-like ancestors. Even Graber, who, as I think, ascribes too great importance to the saccate shape of the first abdominal appendages, nevertheless considers it probable that the ancestors of the Insects were Myriapod-like, and admits that this supposition appears *à priori* to have most to be said in its favour. If, however, we weigh the great differences between the Crustacea on the one hand and the rest of the Arthropoda on the other, a close relationship between Insects and Crustaceans appears simply impossible. The *Nauplius*-form of larva, an exclusively Crustacean possession, the remarkable resemblance in embryonic development between Insects and *Peripatus*, and the constitution of the respiratory and excretory organs, are facts which all compel us to conclude that the Arthropod type is at least diphyletic in origin. The Crustacea, indeed, are to be derived from marine Annelids, which in the course of their development passed through the Trochosphere stage (which in the Crustacean development became transformed into that of the *Nauplius*), while for the ancestors of the Tracheata we must look to terrestrial or freshwater Annelids, more of the Oligochæte type. The subtype Tracheata is at present rejected by several zoologists, since the Arachnids are separated from the rest of the air-breathing Arthropods and approximated to the Pœcilopods. I have above already adduced the evidence against the establishment of the groups Acerata (Kingsley) and Antennata (Lang), and here need only add that the mode of development of the respiratory organs of the Arachnids (Schimkewitsch §, Morin ‖) tells, in

* Nassonow, "Zur Morphologie der niederen Insekten," Nachr. der Moskauer Ges. der Freunde der Naturwissenschaft &c., Bd. 52, Lief 1, 1887 (in Russian).

† Grassi, "I progenitori dei Miriapodi e degli Insetti," Atti Accad. Gioenia Sc. N. Catania, (3) vol. xix., 1886, 83 pp. 5 plates; Bull. Soc. Ent. Ital. 1886, pp. 173–180, tt. 7, 8; Atti Accad. Lincei, (4) vol. iv., 1888, pp. 543–606, 5 plates.

‡ Oudemans, 'Beiträge zur Kenntniss der *Thysanura* und *Collembola*,' Berlin, 1889.

§ Schimkewitsch, "Étude sur le développement des araignées," Arch. de Biologie, t. vi., 1885, pp. 515–584, pls. xviii.–xxiii.

‖ Morin, "Zur Entwicklungsgeschichte der Spinnen," Biol. Centralbl. vi. Bd., 1887, pp. 658–663.

my opinion, decidedly against the union of the Arachnids and Pœcilopods. It is indisputable that *Limulus* has very little in common with the Crustacea (the Trilobites and Merostomata excluded), and that the origin of the Arachnida is enshrouded in thick darkness; but the facts at our disposal appear rather to warn us against the dissolution of the subtype Tracheata and the union of creatures so heterogeneous as the marine Pœcilopoda and the terrestrial air-breathing Arachnida.

LVI.—*Preliminary Descriptions of new Species of* Madrepora *in the Collection of the British Museum.*—Part II. By George Brook, F.L.S.

When just a year ago I published in this Journal preliminary descriptions of a number of new species of *Madrepora*, I anticipated that by the present time a revision of the whole genus would have been ready for press. Considerable delay has been caused by the acquisition of further collections, particularly of the fine series of specimens from the Great Barrier Reef area collected by Mr. Saville-Kent, and of a further selection of specimens from the Macclesfield Bank, collected by Mr. Bassett-Smith, Surgeon R.N. Before these were received a number of the species now described were diagnosed from specimens in the general collection, the distribution of which is increased by their occurrence in the newly-acquired material. As the work of revision is not yet complete, I take the present opportunity of giving short descriptions of forty new species. I believe that the characters indicated will be found sufficient to distinguish the species, although in some cases this may not at present appear to be the case, owing to the lack of precision in many of the descriptions of older species. This I hope to rectify as far as possible in the revision of the genus, the publication of which will not, I trust, be further delayed.

Madrepora ambigua.

Corallum subhorizontal (? suberect), somewhat flabellate; branches irregularly confluent, basal parts fused into a solid mass. Branches 1·5 centim. diameter, with a few short arched and blunt divisions on the upper surface. Apical corallites scarcely prominent, 2·5 to 3, rarely 3·5 millim. diameter. Lateral corallites irregular and very unequal, many immersed; prominent ones chiefly spout-shaped, spreading;